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Evidence that helping at the nest does not result in territory inheritance in the Seychelles warbler

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In an environment that has a shortage of territories, helping to rear younger siblings ('alloparenting') is proposed to facilitate territory acquisition in two ways: (i) through group augmentation that leads to an increase of the territory with subsequent partial inheritance (budding); and (ii) through site dominance that leads to greater success when competing for the natal or a nearby territory after the death of the territory owner (complete territory inheritance). Most young Seychelles warbler (*Acrocephalus sechellensis*) males either show alloparenting or budding behaviour. Future budders had significantly more aggressive interactions with neighbours and assisted their parents more with territory defence than similarly aged future alloparents or non-helpers. This led to an increase of the natal territory of future budders before actual budding took place, whereas the natal territories of future alloparents remained constant in size. Alloparents never became budders and vice versa, refuting partial inheritance as an advantage of alloparenting. Natural male breeding vacancies were never inherited by alloparents born on vacant or other territories, but were inherited by budders born on the vacant territory or, if these were absent, predominantly by budders from neighbouring territories. We offer explicit experimental evidence against the 'helping at the nest to inherit' hypothesis. Experimentally created male breeding vacancies, with both a male alloparent and a similarly aged sibling budder present simultaneously in the vacant territory, were filled by budders only. Site dominance over territory inheritance is linked to budding and not to alloparenting.

Keywords: helping; budding; territory inheritance; group augmentation; site dominance; Seychelles warbler

1. INTRODUCTION

In 3.2% of extant bird species, offspring remain with their parents on their natal territory, often beyond the time of sexual maturation (Emlen 1995; Cockburn 1998). Most of these offspring help to feed the other young of their parents, through which they can indirectly increase the number of their genes in future generations (Hamilton 1964; Vehrencamp 1979; Emlen 1984; Brown 1987). However, direct benefits to these alloparents have been postulated too. The act of helping to rear younger siblings (alloparenting) might lead to site dominance and, hence, to a greater success when competing for the natal or a nearby territory after the death of the territory owner ('complete inheritance'; Zahavi 1976; Woolfenden & Fitzpatrick 1978, 1984; Lindström 1986; Stacey & Ligon 1987; Zack 1990; Koenig *et al.* 1992; Balshine-Earn *et al.* 1998). Alternatively, by enhancing the reproductive success of the breeders, alloparents increase the size of the family unit ('group augmentation'; Emlen & Wrege 1989; Emlen 1991). Larger groups are in a better position to outcompete smaller ones at territorial boundaries, by which the size of the natal territory is expanded. Large territories increase the likelihood that the former alloparent will be able to 'bud off' a portion of the enlarged territory as a breeding territory for itself ('partial inheritance'), which might additionally act as a stepping stone for inheritance of the natal territory (Emlen 1991). However, it is unknown whether the benefit of territory acquisition is linked to alloparental care ('helping at the nest to inherit') *per se*, or a passive effect of delayed dispersal alone (Blackwell & Bacon 1993; Emlen 1994, 1995). In some species, extra individuals (e.g. their own offspring) remain within the breeders' territory but do not help at the nest (Veltman 1989; Sydeman 1991; Caffrey 1992; see also Curry 1988; Poiani 1994). These individuals might still act as budders, which bud off a portion of the natal territory as their own.

Competition over territory vacancies might be mediated by aggression, but it might be (partly) solved by stable dominance hierarchies (e.g. Wiley & Rabenold 1984; Harcourt & Stewart 1989; Von Siemens 1990). In this context, the knowledge of which individual will inherit a vacant territory in relation to its age and previous dispersal/helping status is crucial for our understanding of delayed dispersal and alloparental care (Ragsdale 1999). Unfortunately, in many cooperatively breeding species, non-dispersing individuals switch between alloparenting and non-alloparenting strategies (Stacey & Koenig 1990; Koenig *et al.* 1992), thus making it difficult to disentangle the effects of these strategies in the acquisition of a vacant territory. Also, few studies have proceeded long enough to investigate quantitatively the process of territory inheritance (Chepko-Sade & Halpin 1987; Arcese 1989; Emlen 1995), and experimental studies under natural conditions have yet to be carried out (Emlen 1991, 1995; Balshine-Earn *et al.* 1998). In this study on the Seychelles warbler (*Acrocephalus sechellensis*), we test the 'helping at the nest to inherit' hypothesis.

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The Seychelles warbler has a high annual adult survival (81.1%, 334 birds). Most young birds are excluded from breeding owing to intense competition over breeding territories (Komdeur 1992; Komdeur & Edelaar 2001) and often remain on their natal territory. Alloparents are mainly females (88%, $n=125$), which increase their lifetime reproductive success through indirect benefits and parental experience (Komdeur 1996). Out of the young males that remained on their natal territory, and which had a chance to provide alloparental care (because their parents had produced a subsequent nest; $n=68$), only a few did so (22.1%). Out of all the remaining young males, most (77.8%, $n=81$) budded off a portion of their natal territory for themselves in which to live and if possible to breed, although reproductive success in these territories is negligible (Komdeur & Edelaar 2001). The acquisition of a territory with high reproductive potential always occurs after the death of a territory owner of the same sex (Komdeur & Edelaar 2001), and budders remain to compete over these vacancies. We focus on males because, in contrast to females, only males become budders (Komdeur 1991) and they do not switch between alloparenting and non-alloparenting strategies (Komdeur 1994*a*; Komdeur & Edelaar 2001). Alloparenting males never became budders ($n=15$) and budders that had a chance to provide alloparental care before they became budders never did so ($n=53$) (Komdeur & Edelaar 2001). Here, we provide data on natural patterns of territory acquisition from a dead relative and from a dead non-relative (both viewed as inheritance) in the Seychelles warbler. Additionally, we tested experimentally whether territory inheritance is linked to alloparenting or to other strategies. The Seychelles warbler is an ideal species in this respect for three reasons: (i) the simultaneous presence on the natal territory of alloparents and non-alloparents, (ii) the absence of switching between these strategies, and (iii) the fact that acquisition of a suitable territory for breeding always occurs through inheritance after the death of the territory owner.

2. MATERIAL AND METHODS

(a) *Study population and data collection*

The entire population of Seychelles warblers on Cousin Island (04°20′S, 55°40′E; 115–123 groups, 310–400 birds) was under study from December 1982 to October 1996. Between 23 and 29 September 1988, 29 colour-ringed adult warblers (16 males and 13 females; all 3–5 years old) were transferred from Cousin Island to Aride Island by motorboat to establish a new population. On Aride, all breeding groups and their male offspring were studied from September 1988 to March 1997. Data are based on individually colour-ringed males, ringed as nestlings in high-quality territories (high numbers of insect food available; for methods, see Komdeur (1992)), of which the dispersal and settlement patterns were monitored monthly after hatching. As warblers rarely colonize other islands by themselves (out of 2156 ringed adults, only one bird (0.05%) is known to have flown from Cousin Island to Cousine Island), we assumed that missing birds had died if they were not found on the same island. After the males have reached the age of 12 months (age at maturity), we documented the status of each male each month during his entire life: an alloparent or non-alloparent on the natal territory; a budder, which has acquired and defends part of the parental territory; a floater, which wanders over the island without permanent residence; or a breeder, which has a breeding territory with a female partner. Young males (10–12 months old) that ultimately adopted the alloparental or budder status are termed future alloparents or future budders, respectively. Young males that have never been alloparents or budders and that would ultimately become floaters or breeders after reaching one year of age are grouped under the term 'other'. All territories were checked regularly during 1 h (every two weeks: 1985–1991; every four weeks: 1982–1984, 1992–1997) for presence of colour-ringed birds, to assess dispersal and survival of birds, and for reproductive activities. In 35 territories that contained three birds only (the breeding pair and its male offspring of 10–12 months old), we recorded the frequency of territory disputes, and the identity of all the warblers participating in these disputes, during 1 h when the young male was 10, 11 and 12 months old. We determined size of the natal territory when the focal male was born and when 12 months old. Territory boundaries were identified by playing recorded song at different locations to provoke territory defence behaviour by the focal birds. Territory size was assessed using a compass and aerial photographs. We used a genealogy based on putative parents to determine the degree of relatedness between all males (potentially) competing for a vacancy, and the relatedness between these males and the breeding pair on a given territory. If breeding vacancies were taken by 1-year-old males, these males were grouped under the term '1 year old' because at this age it is not yet possible to establish their status (e.g. alloparent or budder).

(b) *Experimental removals*

To test the 'helping at the nest to inherit' hypothesis, we selected nine territories on Cousin Island that contained a breeding pair, a male alloparent and a male budder in an adjacent 'budded' territory. For each territory, the alloparent and the budder were full-sibs. The breeding male was removed from these territories and translocated to either Aride during the period 23–29 September 1988 ($n=4$) or Cousine during the period 29 June–1 July 1990 ($n=5$) (Komdeur 1994*b*). Experiments in the same period were never carried out within a distance of four territories of each other. After the removal of the breeding male, the focal alloparent and budder were observed on successive days until the breeding vacancy was filled.

(c) *Statistical analyses*

Differences in aggressive behaviour between trio-groups with future budders, future alloparents or 'other' males, were tested by means of a Kruskal–Wallis test because these data were not normally distributed within categories. For convenience of analysis, the effect of male status and affiliation with the vacancy (born or not born on vacant territory) on the outcome of the competition over a vacancy was tested by selecting territories that had zero or one candidate males present on the vacancy and zero or one candidate males present in adjacent territories. If two candidate males were present simultaneously, these males were always of a different status. Non-random occupation was tested by using the binomial distribution, with the probability of occupying the vacancy at 0.5 (H_0: each bird has equal probability) for each status category. When this hypothesis was rejected, we calculated the one-tailed confidence interval for the probability of occupying the vacancy for that category of bird that mostly filled the vacancies. For all tests carried out, the probability values are two tailed and the null hypothesis

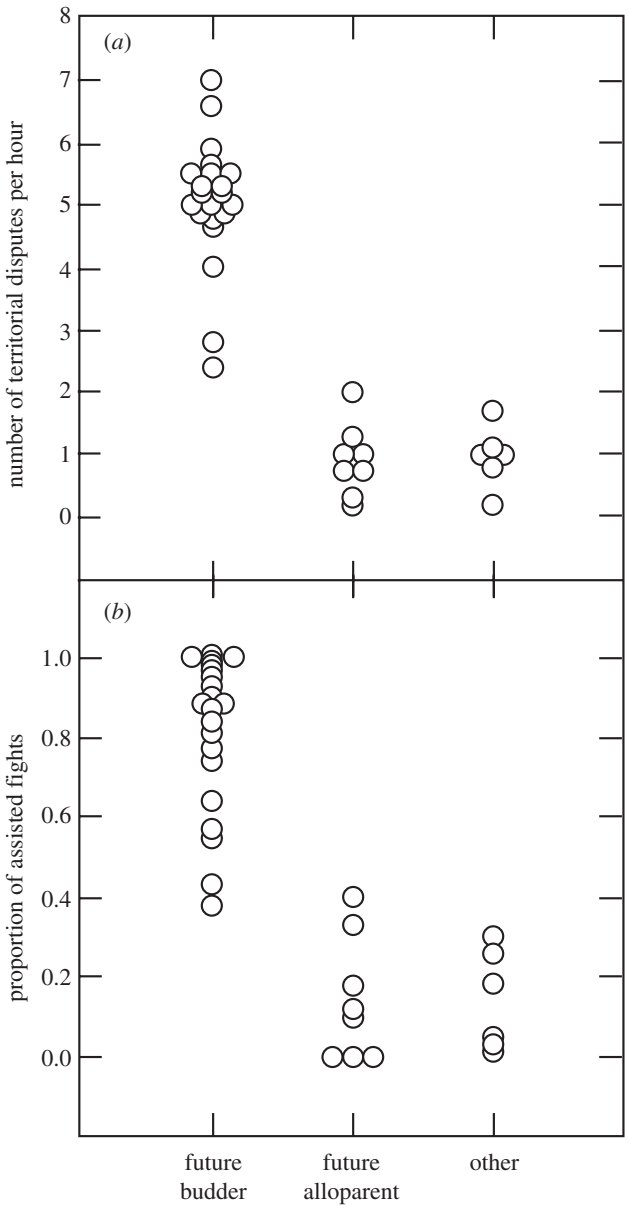

Figure 1. Agonistic interactions observed in Seychelles warbler territories with a breeding pair and one 10–12-month-old male offspring in relation to the future status of this male offspring. (*a*) The frequency of territorial fights (difference between groups: Kruskal–Wallis test statistic, $H = 24.61$, d.f. $= 2$, $p < 0.001$). (*b*) The proportion of fights in which the young male assisted his parents (difference between groups: $H = 24.21$, d.f. $= 2$, $p < 0.001$). Status of young male: future budder ($n = 21$), future alloparent ($n = 8$) and 'other' ($n = 6$).

was rejected at $p < 0.05$. All calculations were done using SYSTAT v. 7.0.

3. RESULTS

(a) *Male status, aggression and change in natal territory size*

In groups comprising the breeding pair and one male offspring, significantly more territorial disputes were observed in territories with a 10–12-month-old future budder than in territories with a similarly aged future alloparent or 'other' male (figure 1*a*). In addition, these

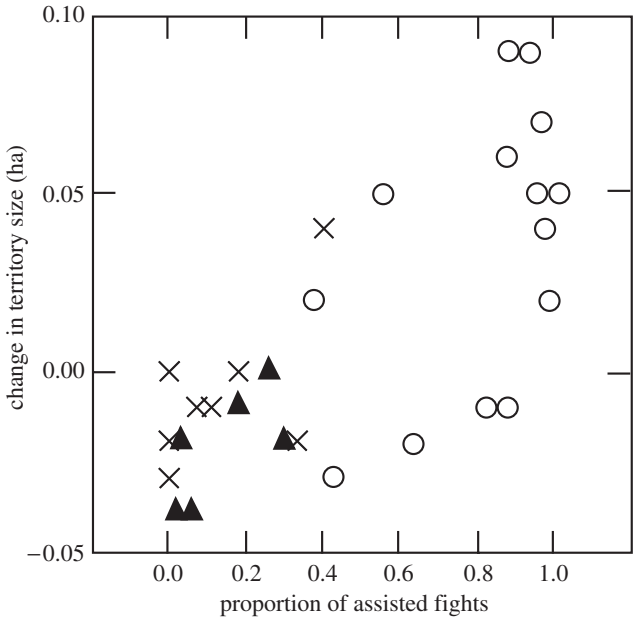

Figure 2. The relationship between the change in natal territory size from the year of hatching to the next year (y-axis) and the proportion of assisted fights (x-axis) by 10–12-month-old Seychelles warbler males (future budder, $n = 14$ (empty circle); future alloparent, $n = 8$ (cross); or 'other', $n = 6$ (filled triangle)) ($y = 0.051\ x - 0.028$). The proportion of assisted fights was square-root arcsine transformed (in radians) before carrying out a step-down multiple regression, excluding all non-significant terms and their interactions in the order of their significance (proportion of assisted fights: $F_{1,27} = 31.0$, $p < 0.001$; future status of male: $F_{2,25} = 0.74$, $p = 0.49$; frequency of territorial disputes (per hour): $F_{1,24} = 0.06$, $p = 0.81$; status × territorial disputes: $F_{2,22} = 0.71$, $p = 0.51$; proportion of assisted fights × territorial disputes: $F_{1,21} = 0.12$, $p = 0.73$; status × proportion of assisted fights: $F_{2,19} = 2.30$, $p = 0.13$; three-way interaction: $F_{2,17} = 0.22$, $p = 0.80$).

future budders assisted their parents significantly more with territory defence than future helpers or 'other' males (figure 1*b*). The change in territory size was positively related to the proportion of assisted fights, but independent of the frequency of territorial disputes, of the future status of the male, or of any of their interactions (figure 2). The change in territory size differed significantly between groups, with a male offspring of different future status ($F_{2,26} = 8.91$, $p = 0.001$). Groups with a future budder increased their territories ($t_{14} = 3.50$, $p = 0.004$), whereas groups with a future alloparent maintained their territory size ($t_7 = -0.83$, $p = 0.434$) and territories of groups with an 'other' male decreased in size ($t_6 = -3.31$, $p = 0.020$).

(b) *The outcome of the competition over breeding vacancies*

(i) *The effect of male status and affiliation*

Table 1 summarizes, for Cousin and Aride, which males were present on or adjacent to the naturally occurring breeding vacancy and which male filled the vacancy. On Cousin Island, seven out of the 28 vacancies were filled by 1-year-old, non-alloparenting males from other high-quality territories. It is unknown whether these males were future budders, because the minimal age to

Table 1. Summary of which males were present in an adjacent territory to the natural breeding vacancy, or on the natural breeding vacancy, and which males filled the breeding vacancies on the islands of Cousin and Aride.

(A related male is a son of the breeding pair previously present on the vacancy. An unrelated male is not a son of the breeding pair previously present on the vacancy. Plus signs indicate birds that were present; minus signs indicate birds that were absent; *n* is the number of occurrences.)

territory	strategy	Cousin	Aride
present at adjacent territory	related budder	+ + − − − − −	+ + −
	unrelated budder	− − + + − − −	− − +
present at vacant territory	related alloparent	+ − − − − − −	− − −
	related non-alloparent	− + − + + − −	+ − −
	related floater	− − − − − + −	− − −
	none	− − + − − − +	− + +
new owner	related budder	+ + − − − −	+ + −
	unrelated budder	− − + + − − −	− − +
	unrelated 1 year old	− − − − + + +	− − −
	n	6 1 13 1 1 2 4	4 12 1

become a budder is 1 year (Komdeur & Edelaar 2001). The other 21 vacancies were filled by budding males born on the vacant or adjacent territories. On Aride Island, all 17 high-quality male breeding vacancies were filled by budding males born on these or adjacent territories. In the case that a budder, born on the vacant territory, was present in a territory adjacent to the vacancy, the vacancy was always filled by this male (Cousin: $n=7$, binomial test, $p=0.016$, confidence interval (CI) = 0.65–1.00; Aride: $n=16$, binomial test, $p<0.001$, CI = 0.83–1.00; both islands combined: $n=23$, binomial test, $p<0.001$, CI = 0.88–1.00). In some of these cases, a non-budding contestant was born and present on the vacancy, but he never occupied the vacancy (Cousin: $n=7$, binomial test, $p<0.016$, CI = 0.65–1.00; Aride: $n=4$, binomial test, $p=0.125$; both islands combined: $n=11$, binomial test, $p<0.001$, CI = 0.77–1.00). Alloparents that were born and present on the vacancy never occupied the vacancy (Cousin: $n=6$, binomial test, $p=0.016$). Even in the absence of a budder born on the vacancy, non-budding males (non-alloparents present on the vacant territory, $n=2$; floaters, $n=2$) never inherited the vacancy. Instead, one vacancy was filled by an unrelated budder from an adjacent territory and three were filled by 1-year-old males (but it was unknown whether these were future budders) from other high-quality territories (non-budders born on the vacancy versus birds not born on the vacancy, $n=4$, binomial test, $p=0.125$).

If an alloparent and a full-sib budder were present on the vacancy, the vacancy was always filled by the budders. On Cousin Island, all of the six naturally occurring male breeding vacancies that contained both an alloparent and a fully related non-alloparenting budder were filled by the budder (binomial test: $p=0.031$, CI = 0.60–1.00). In addition, all of the nine experimentally created male breeding vacancies that contained both an alloparent and a non-alloparenting full-sib budder were filled by the budders (binomial test: $p=0.004$, CI = 0.72–1.00; combined with the data from Cousin: $p<0.001$, CI = 0.82–1.00). All 15 alloparents in this data set eventually died without having acquired a breeding territory.

(ii) *The effect of male age*

On naturally occurring vacancies on Cousin, there was no significant difference in the age of the budder that occupied the vacancy and the age of the full-sib alloparent that was present on the vacant territory (paired $t_5=-0.67$, $p=0.53$). This was also true for the experimental removals on Cousin: there was no significant difference in the age of the budder that inherited the vacancy and the full-sib alloparent that was present on the vacant territory (paired $t_8=-0.26$, $p=0.80$). Combining natural and experimental data on alloparents that contest with full-sib budders on Cousin did not change the result (paired $t_{14}=-0.64$, $p=0.53$). Age did not differ between successful and unsuccessful contestants when including non-alloparenting or floating contestants (paired $t_{19}=-1.23$, $p=0.23$) or when including data from Aride (four non-helping males) (paired $t_{23}=-0.36$, $p=0.72$).

4. DISCUSSION

(a) *Territory inheritance by alloparents and budders*

Our study shows convincingly that both the partial and the complete inheritance of a territory are not linked to alloparental care (contrary to the 'helping at the nest to inherit' hypothesis). (i) Partial inheritance of the natal breeding territory by an alloparent never occurs because alloparenting males were never observed to become budders. Moreover, compared with future budders, future alloparents assisted their parents little in territorial disputes and did not increase the size of the territory, which would have facilitated subsequent partial inheritance. (ii) Complete inheritance by alloparents of their natal territories after death or experimental removal of their father was never observed. In addition, most alloparents died (85.7%, $n=21$; this study, 15 alloparents from this study and 6 alloparents from another study (Komdeur & Edelaar 2001)) without having acquired a breeding territory. Instead, territory inheritance is almost exclusively linked to budding. (i) Most breeding vacancies were filled by budders; the rest were filled by 1-year-olds that were too young for us to establish their future strategies, but they might have become budders. (ii) All naturally and experimentally created male breeding vacancies on the natal territory that had both a budder, which was born on the vacancy but present in an adjacent territory, and an alloparenting male sibling (both fully related to the previous breeding pair) were only filled by the budder (with no effect of age). We therefore conclude that budding, and not alloparenting, is the strategy that increases the probability of acquiring a high-quality breeding territory.

(b) *Territory inheritance in relation to male affiliation, age and status*

In the Seychelles warbler, territory inheritance not only depends on male status, but also is linked to affiliation. If a budder was present next to a breeding vacancy, the vacancy was always taken by this budder and never by budders from more distant territories. If neighbouring budders were absent, the position was taken from outside by 1-year-old males. We think that this occupation pattern is not due to an incomplete knowledge of vacancies by males of other categories or from territories further away. Radio-telemetry studies showed that young males, including alloparents and budders, do sample different territories all over the island at least once a day (J. Komdeur, V. Madsen, J. M. Tinbergen and S. Daan, unpublished data).

Age-related dominance for access to breeding positions by males has been shown in many cooperative breeders (e.g. Wiley & Rabenold 1984; Curry 1988; Rabenold 1990; Kullberg & Angerbjorn 1992; Nakamura 1998). In the Seychelles warbler, unusually for cooperatively breeding birds (Poiani 1994), dominance over territory inheritance is independent of the age of the male, but is highly related to male status (see also §4(a) above) and affiliation. It is potentially easy for a budder or alloparent to fill a vacant breeding position, because territory 'switching' by territory holders rarely occurs. Nearly all the breeding birds (99.1%, $n = 314$) remained in their territories until their death and thus never occupied vacancies in territories of higher quality where they could obtain a higher lifetime reproductive success (Komdeur 1992; Komdeur & Edelaar 2001). This inflexibility of established breeders, despite the possibility of higher reproductive success elsewhere, is common in some species (Picman 1987; Korpimaki 1988; Aebischer & Coulson 1990; Ens *et al.* 1995), but not in others (Krebs 1971; Newton & Marquiss 1982; Beletsky & Orians 1987; Curry 1988). Kokko & Sutherland (1998) predicted that if territory 'switching' is absent, the relative advantage of budding increases.

The absence of territory 'switching' and the presence of local precedence over territory inheritance without an effect of male age indicates why it pays for Seychelles warbler males to stay and bud in a saturated environment. We favour this explanation because it seems to be the most parsimonious. It is unclear why some males have the high-fitness-related budding strategy and others have the low-fitness-related alloparenting strategy. Apart from several maladaptive explanations (see, for example, Wright 1999), there might be differences between individual males in which each male carries out the strategy that maximizes his fitness. Budding males showed higher levels of aggressive behaviour compared with other males, which could be related to (fighting) quality. Alternatively, or perhaps in combination with the former explanation, males might find themselves in different competitive environments. For example, a male might forego the otherwise high-fitness-related budding strategy when several budders are already present near the natal territory and local competition over the future vacancy is expected to be high. Both hypotheses can be examined through manipulation of individual quality or of the number of competing budders. However, ways to directly influence individual dispersal and alloparenting behaviour need to be developed so that their fitness effects can be determined.

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